4

On the Survival Value of Fish Schools

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INTRODUCTION

THE QUESTION of whether the typical schools or other groupings of fishes have survival value has often been raised, but few investigators have gone into the matter in any depth. One approach, which might be called the anecdotal or the naturalist's approach, is usually given as a general verbal interpretation, based on simple observation. Another, which might be called the mathematician's approach, is typically given as a rigorous analysis of a schematic abstraction of a fish school, usually as an oversimplification, in which prey and predators are considered as making more or fewer encounters, based primarily on random movements. The first may be exemplified by Breder and Halpern (1946), Hiatt and Brock (1948), Sette (1950), Springer (1957), Milanovskii and Rekubratskii (1960) and von Wahlert (1963). The second may be illustrated by Brock and Riffenburgh (1960) and Olson (1964). There is, of course, merit in both these approaches, but neither, by itself, would seem to be adequate to develop a full understanding of the phenomenon. A third approach would, of course, be the experimental one, but there have been only two reports directed toward the possible significance of schools to survival (Williams, 1964; John, 1964). The recent great activity in the study of schooling, on aspects other than possible survival value, has nonetheless useful data to contribute to this subject.

The primary purpose of the present paper is to indicate clearly that all fish schools are not necessarily similar structures, nor that they could be encompassed in a single formulation. A considerable amount of material has been examined and various theoretical considerations have been drawn into the present study. This treatment makes it possible to show, at least at minimum, some of the complications necessarily involved in any attempt to assign a specific survival value to a given fish school under definite conditions of existence.

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DEFINITIONS

As in most fields that are undergoing rapid growth there is considerable variety in the usage of words and terminology. This is a normal symptom of an active and changing field. It is brought about primarily by differences in the interests and purposes of the earlier writers on the subject. Evidently there are still too many new facts and ideas developing to expect an early stabilization or general agreement on usage. Thus it behooves all workers in the area to indicate scrupulously just how they are using any terms that could possibly lead to confusion and misunderstanding. Also readers should use great care to be sure that they understand an author's precise meaning. In addition to definitions in this section, differences in point of view and usage are indicated wherever clarification would seem needed.

The word "school" has a long history of common usage in connection with fishes and many dictionaries give as a definition, "a large number of fish swimming together," or some equivalent. The connotation would ordinarily be that if they were swimming together they would be going in the same direction, as opposed to churning about or simply resting. Parr (1927), Atz (1953) and Breder (1929 through 1965) have used the word essentially in the sense of the ordinary dictionary definition. Spooner (1931) attempted to restrict the use of "school" to cover only social groups, as opposed to groups drawn to one place by non-social influences. Certainly there is no objection to redefining a word for technical purposes when such a modification of usage is justified. However, it is seldom possible to determine what motivations are effective in the formation of a school. In most cases it is difficult or impossible to define what determines the formation of any type of fish group. There is always at least a residue of both a social and non-social influence present for the fishes must at least tolerate each other and must be located where they are because of non-social influences, such as temperature, nearness to surface or bottom, light, *et cetera.*

It is partly for the above reasons that the more nearly objective and always recognizable measure, not concerned with what drives the fish may or may not have, has been used here. Williams (1964) objects to this usage stating, "It may be of some value to distinguish these two phases of activity,[1] but the difference between social and non-social groupings is in greater need of terminological distinction." This, of course, is a measure of the difference between two approaches, needs and purposes. It very nicely illustrates the point made in the preceding comments. The field is still in such an uncongealed state that it is possible for two very thoughtful papers (Brock and Riffenburgh, 1960; Williams, 1964) to express essentially opposite points of view.

Milanovskii and Rekubratskii (1960) who consider ". . . schooling behavior as one of the adaptive features of a population of a single species . . ." use the word "school" in an even broader way than does Williams and indicate that the usages of Parr, Keenleyside (1955) and others are "one-sided" and "contain mechanistic elements." At least there is agreement in the present paper with their comment, "At any stage of elaboration of the problem we find it necessary to have a working hypothesis—tentative definitions of school and schooling behavior, which should be based on the present level of our knowledge."

Williams (1964) develops the idea that schooling and aggregating are basically rooted in a tendency to hide behind something, as a response to "fright." He carried out experiments bearing on this idea, with a number of species of essentially aggregating types of fishes, as did John (1964) on *Astyanax.* Both found that in a "blank" environment their fishes tended to stay together and formed aggregations or "fright schools." With these experiments there is no disagreement, but an examination of them may help to further clarify the different usages and attitudes toward the word "school." If the correspondingly opposite experiments be made of placing permanently-schooling fishes in an environment of abundant and varied cover these fishes will not hide behind anything, even if completely isolated from others of their kind. They merely go into a period of fast and erratic swimming, evidently in search of companions —behavior that looks surprisingly like "panic." It is not uncommon for them to exhaust themselves, collapse and promptly expire. For this reason the term "obligate schoolers" would seem to be appropriate in contrast to fish that may be called "facultative schoolers." Under such conditions of isolation, obligate schoolers will attempt to school with practically any fish, solitary or not, that may be presented. These may be very unlike, for example, *Mugil* "schooling" with *Canthigaster* (Breder, 1949). Evidently it is the motion of another swimming fish that induces the otherwise isolated obligate schooler to react, while they do not respond at all to inert objects. Formal experiments hardly seem necessary in this connection, as the action seems to be entirely evident. The attempt to experiment with these extreme types is, in any case, difficult. They are notoriously difficult to even establish and keep in aquaria. This is the principal reason why scombriform, carangiform or clupeiform species are seldom seen on display in public aquaria.

Williams performed his experiments on *Anguilla rostrata* (LeSueur), *Hyphesobrycon flammeus* Myers, *Notropis antherinoides* Rafinesque, *N. stramineus* (Cope), *Pimephales notatus* (Rafinesque), *Xiphophorus* hybrids, *Poecilia reticulata* Peters, *Lepomis cyanellus* Rafinesque and *Colisa lalia* (Hamilton-Buchanan).[2] Not

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[1] That is, "schooling" and "aggregating" in the sense used here. This footnote mine.

[2] Breder and Halpern (1946) and Breder and Roemhild (1947) performed somewhat related experiments in which they analyzed the statistical deployment of a number of similar species of fishes, none of which were obligate schoolers. All such work on aggregating forms, while useful, is not adequate to determine the behavior of obligate schoolers.

one of these is an obligate schooler. They may form aggregations in the non-polarized sense, fright schools, schools in rapidly-flowing water or other facultative assemblages. If this was all there was to the matter no one would have thought to differentiate chronic schoolers from the others. It is here that the confusion about this term and its usage arises. In an attempt to clarify the present point of view, the following details are brought together to enable a perhaps clearer separation of the obligate from the facultative.

To be considered obligate, schoolers must be coherently polarized; can only be forced to stop schooling momentarily, and then only by means of considerable violence; and will not maintain a state of random orientation. The group is permanent, excepting only when physical conditions in the environment suppress the functioning of some essential system, usually the optical, as on an extraordinarily dark night. Isolated members display erratic locomotion and commonly cannot exist for long in the solitary state. The drive to associate with others in a body of great unanimity of orientation is clearly a positive matter of great strength, quite unlike the fragile schools of fright, or other temporary mutual orientations seen in fishes which otherwise are found more commonly in non-polarized aggregations or as solitary individuals. For fully evident mechanical reasons only schooling fishes are able to form fish mills, a type of circular swimming which occurs regularly in obligate schools. The non-polarized aggregations are fully unable to form the mill structure. See Breder (1965) for an extended discussion of this phenomenon.

In the terminology proposed by Williams, "school" refers to any group of fishes ". . . that owes its persistence to social (but not sexual) forces" and "aggregation" refers to ". . . groups that arise by individuals independently seeking the same localized conditions", which is in agreement with Spooner (1931). Probably all groups contain an element of both "school" and "aggregation" in the above usage, except the obligate schoolers, as here used. That is, the obligate schooler is so locked to its fellows that it ignores other things in its environment to a remarkable extent while the facultative schooler clearly is more actively involved with other environmental details, often ignoring his fellows to the point of losing its group altogether. Of this Williams was aware when he wrote that ". . . when one observes a dense concentration of the same species moving about in a pelagic or other uniform habitat . . . he is probably safe in calling it a school . . . ," but that "schools and aggregations cannot be as confidently distinguished in heterogeneous environments, and it must often happen that groups are formed that owe their cohesiveness to both schooling and aggregation in mutual reinforcement (heterogeneous summation of Tinbergen, 1951)."

Thus it appears that what would seem to be two very different positions are not as far apart as might be thought for, in many cases, if not all, by designating species by either system a very similar listing would develop. That is to say, what are designated as schools in the present view are assembled on a great preponderance of social tendencies, while aggregations are assembled with a far greater content of general environmental influence. This is precisely the view propounded by Williams, and in an area where so little is yet known, may be very useful as a first approximation on what holds the group together, that is, primarily social influences or non-social influences.

ANALYSIS OF PERTINENT DETAILS

The treatment of the available data in this section has been broken down into several subsections, bringing together the controlling influences of the environment and their effects under various conditions of predation.

THE INFLUENCE OF ENVIRONMENT

A suitable point of departure is a consideration of the sensory modalities that are dominant in schooling fishes and the effects of various environmental influences on their functioning.

Visibility and transparency of water

It has been abundantly shown that vision is necessary for the formation and maintenance of fish schools, see for instance, Parr (1927), Atz (1953), Breder (1959), and Blaxter and Parrish (1965). Also, blind fish and fish in total darkness are unable to maintain this highly polarized arrangement. Obviously the transparency of the water is of great importance to any behavior so largely dependent on vision. This was clearly recognized by Brock and Riffenburgh (1960), in connection with vision's role in school maintenance, when they wrote, "A consideration of the optical peculiarities of water is pertinent in this connection. The distance an object of given size can be seen depends upon two factors: the intercept angle at the eye and the contrast difference between the object and the background. Due to backscatter and light absorption an object of high contrast will fade from sight regardless of size at a relatively small distance, say 200 feet or less, even in the clearest water. This means that for objects above a fairly moderate size, large enough to give an intercept angle adequate for effective vision at the distance where light absorption and backscatter reduce contrast difference to a point of invisibility, taken at 2 per cent, for man (Duntley, 1952), any increase in size of the object will not effectively increase the distance at which it may be seen. The critical intercept angle for the human eye is taken to be one minute which would occur for an object 0.72 inches in diameter at 200 feet." This obviously gives a measure of the extreme visibility range under water, which in most places is not even closely approached. It may be that this estimate, although based on Duntley's paper, is too high, for he, in another place, wrote, "It is expected that water having hydrological range[3] as great as 130 feet will be found in the Sargasso Sea and in the Mediterranean." In a personal communication, Dr. Eugenie Clark estimated that horizontal visibility as great as 180 feet occurred off the Caribbean coast of Yucatan.

Before distances as great as those mentioned above are brought into the discussion, there are considerations involving the geometry of fish schools operating completely within the area of full visibility, which can properly be discussed at this point. Since fish often tend to accumulate into "balls," see for instance Breder (1959), they thereby also tend to occupy the minimum space and show the least surface area. This is also done by a droplet of fluid for purely mechanical and geometrical reasons. The result is to incidentally produce a figure of least conspicuousness and therefore to possess some presumed selective value. This we might call "primary selective value," in which the *direct* response to a stimulus, which may be a simple physical condition, produces a result of definite selective value. Viewed this way, it follows that departure from the spherical form may be taken as a measure of the extent to which other influences make the fishes independent of this or other similar constraints. In its place come other constraints, which may be thought of as "secondary survival values." These are, of course, the types of selective activity ordinarily referred to as simply "selective values," by evolutionists. When the primary and secondary selective processes both press in the same direction, it is often difficult, if not impossible, to clearly separate them, but it is here that one would expect the development of great stability of behavior or structure or whatever the selective processes have been directing. Anyone familiar with schooling fishes can attest to the strength and rigidity of the habit. Departures from it are clearly associated with special circumstances. Some of these may be considered merely various deformations of a primary tendency toward a globular school, or even a non-polarized aggregation, for in this feature both schools and aggregations show similar tendencies.

Deformations may be related to groups forming close to the water surface and spreading out like a rising globule of very viscous oil. A similar case, on the bottom, would be like a globule of heavy oil spreading out. In very shallow water both surface and bottom would exert deformative influences. Also elongate schools are normally associated with fish migrating or under other kinds of highly directional travel.

As a more generalized concept of the geometry of schools, their size and the restrictions of lateral visibility in water, the following situation may be postulated. Given a case where a single individual, prey or predator has a useful visual range of, say, 30 feet, each solitary individual fish may be considered at the center of a sphere with a 30-foot radius. This is too much of an oversimplification, however, for the restrictions on vision from above and below are somewhat less than in any horizontal direction. In the case of looking down, an object below is more fully illuminated than any side view of one at the same depth. In the case of looking up, the fish is silhouetted against the illumination from above. The resultant increase of visibility, both up and down, increases the visual range vertically to an extent determined by turbidity, light angle, *et cetera,* except for the following facts. These differences in visibility, owing to direction, are the precise ones that are minimized by countershading. In most clear open waters countershading is notably efficient. Consequently it is more nearly correct to think of an individual fish as at the center of a geometric figure approximating a very slightly prolate ellipsoid with its long axis vertical and the horizontal axis, coinciding with that of the fish, longer than the transverse axis.

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[3] Duntley (1952) defined "hydrological range" as follows. "The clarity of water can usefully be specified in terms of *hydrological range* (v). This is the distance measured along the path of sight, at which the apparent contrast of any object seen against a deep water background is reduced to two per cent of its inherent value. Along a horizontal path of sight hydrological range (v_o) is related to the transmittance (T) of the water (as measured by a hydrophotometer) by the equation

$$T = e{-}3.912x/v_o \qquad (4.1)$$

where x is the distance from the object to the observer." For the derivation of this expression see the original.

As a matter of simple geometry, several propositions follow. One fish or a "school" of two has practically the same lateral range of vision and there is little increase in the ability of two fish, forming a "school," to detect a predator, over the ability of a single fish. This is because the "inner side" of each is either blocked by its companion or, if not, their fields of view are almost completely duplicative. As a school increases in the number of fishes the range of vision increases proportionately to the area of the side presented. As both prey and predators wander about, there is thus twice the chance of an encounter with two single fish, not encroaching on each other's field of vision, as with two fish together in a school.

The above is precisely calculable and is independent of concerns of Duntley (1952) so long as the fishes do not wander beyond their mutual visibility ranges. Examples cover only certain fishes indigenous to very shallow water, or living near the surface where illumination is not notably attenuated. Here small fishes such as *Jenkinsia* or *Sardinella* are often preyed upon by immature carangids and *Sphyraena* or mature *Strongylura*. The schools may be large, up to over a thousand or more individuals, with the predators cruising about with the prey in full view. The predators may be typically solitary (*Sphyraena*) or in small bands themselves (*Strongylura* and *Caranx*). Any of them may strike into a school and pick off their prey at will, either alone or as two, or rarely a few, actively-feeding predators. In the above named fishes, multiple attacks are most common in the carangids. Presumably the predators under such situations are generally filled to satiation. Field observations have shown that individuals coming in from some distant point beyond the range of visibility, and new to the school of prey, usually pick off a few fish and then rest idly nearby. From then on it is only occasionally that one will dash in to take a single fish, with extended idle intervals between. The length of these intervals is presumably a measure of the degree of digestive satiation which an individual predator has reached. The situation above described is one that can be generally found in regions where such fishes abound and is apparently the normal circumstances under which they usually exist. This could be conceived of as the degenerate limit of the situations involving no limitation on visibility, as earlier discussed. Here the predators are never under prolonged hunger and escape of a school unscathed never occurs. Also here the maintenance of a population of prey species must depend more on reproductive potential or continued recruitment from "safer" environments, with little or no dependence on locomotor activity for escape in flight. However, even within the limits defined, the least healthy, alert or most awkward, would on the average, be systematically eliminated. From the standpoint of selection theory, this in itself could be valuable to the long-time survival of the population.

Sound production and its prevention

The problem of sound production by the swimming efforts of schooling fishes or their predators is presently unclear for several reasons, see for instance Winn (1964), Wodinsky and Tavolga (1964) and van Bergeijk (1964). Ordinarily most fishes make no appreciable sound incident to their locomotor activity but may do so on sharp turns, see Moulton (1960). His observations check well with our own in this respect, considering that different fishes were under sonic observation. Very little on swimming sounds has been reported by acoustical students on either individual fishes or fish schools. This is most notable in observations made in light. It is possible that there has been selection tending to reduce activities and structures responsible for the production of sounds. If this is the case, then schooling fishes that are reported to produce sounds in the dark, see for instance Takarev (1958), Shishkova (1958), Moulton (1960) and Marshall (1962), could represent an overriding nocturnal specialization toward the prevention of too-wide dispersal under lightless conditions. To predators with sonar echo mechanisms, such as porpoises, fish sounds or their absence would apparently make little difference, if any. These forms are able to feed by locating fishes by means of their echo-ranging mechanisms alone, the data on which is summarized by Norris (1964).

The above should not be interpreted to mean that a complete silence is present in a school of fishes, but only that its magnitude is too small to be effective at distances under which predators have to operate. The sounds noted by Moulton (1960) when sharp turns are made by fish schools are evidently only produced under some fright-inducing stimulus. This means only that fish already sensing the near presence of a predator in their locomotor escape efforts, exceed some physical limit above which higher sound levels are reached. This occurs at a time when quietude is evidently no longer as important as flight.

Tavolga, in a personal communication, wrote as follows about the quality of sounds produced by a "smoothly" moving school, "The quality of this noise is interesting in that it would tend to be random since all the fish-tail movements are not perfectly in phase. Such a noise might tend to be masked by ambient noise. Therefore, even if a predator might be in the range of this school noise, he might perceive it as only a slight increase in ambient noise level, as might be produced by wave action or some other physical phenomenon." These sounds would, of course, be quite different from the various nighttime sounds described by authors, often as clicks or taps, and which are clearly not sounds made incidental to locomotion.

A point to be considered about the above is related to the information provided by the sonar instruments such as those used by anglers to locate fishes. These devices, because of the Doppler effect, provide not only an indication of the presence and species but also an estimate of the size of the fish or fishes and the numbers present. This information is based on the pulsations provided by the motion of swimming fishes, which are characteristic for most species and sizes. Of course, the reflected high frequencies used by these instruments, brought down to the audible range by electronic means, are not identical with the low frequency, faint sounds produced by the fishes themselves. However, if these are audible at all, they must have a beat basically similar to that of the ultra-sonic reflected frequencies. It is certainly true that many schools are so lacking in swimming synchronization that only a broad band of low frequency noise could be expected. However, schools vary from those in which the individuals are completely out of phase to those that have well over 50 per cent of the members in good swimming synchronization. Occasionally small schools, usually of not more than a dozen individuals as seen in various species of *Mugil*, *Caranx* and a variety of scombrids, are clearly in near perfect phase. Schools, other than the ones lacking any substantial synchronization, would introduce a type of "noise" containing a beat, more or less masked, but which should be able to convey information to a predator, including estimates of species, size, number and direction of travel. These thoughts introduce an unexplored area, including the extent of synchronization in fish schools, the reasons for its presence or absence and a study of its sonic product, including volume and characteristic beat. All this should be amenable to an instrumental approach. Indeed the schools without individuals in phase may be an adaptation to the need for the suppression of telltale sounds rather than the other way around.

Bearing on this is the question of the ability of fishes to detect the direction from which a sound emanates. It has been argued by Harris and van Bergeijk (1962), van Bergeijk (1964) and Harris (1964) that far-field effects are virtually non-directional for fishes, while near-field effects are highly directional. Thus, a school out of visual range and beyond the near-field might not give a predator sonic cues as to its location, but nonetheless, the sounds might stimulate intensified ranging activities on the part of the predator that could lead the latter to its target on a basis of increasing intensity of sound as it approached the school during random searching. This is a matter distinctly different from following up a sound gradient, the phenomenon whose existence has been questioned by van Bergeijk.

In order to present some idea of the areas and limits of the near-field and far-field effects and their somewhat complicated relationships, the following comments and calculations are given.

How far near-field directional cues extend from a sound producing source will, to a considerable extent, determine their utility to the listener. This distance varies with the frequency, being greatest at low frequencies and least at high, and with the amount of the energy output of the source. For instance, holding the energy output constant, through the temperature range at which *Galeichthys* emits its characteristic "percolator"[4] sound, approximately between 20 and 30°C, a frequency of 1000 Hz has the calculated limit of its near field between 9½ and 9¾ inches from the origin, respectively. Other values in feet follow:

Temp.	Frequencies in Hz				
°C	25	100	200	300	800
20	31′+	7′+	3′+	3′–	1′+
30	32′+	8′+	3′+	3′–	1′+

These relationships were calculated from the given temperatures and frequency by means of the empirical equation of Albers (1960).

$c = 141{,}000 + 421t - 3.7t^2 + 110s + 0.018d$, where c = velocity in cm/sec, t = temp. in °C, s = salinity in ppt and d = depth below surface in cm. Using $s = 34.8$ ptt and $d = 150$ cm, values of c were calculated for various values of t. Changes in s and d were negligible for present purposes and were held at the values given, reducing the equation to

$$c = 145{,}829.7 + 421t - 3.7t^2.$$

The values of the wavelengths were obtained from the relationship

$$\lambda = c/f$$

where λ = wavelength and f = frequency in Hz. From van Bergeijk (1964) the point of equal

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[4] So designated by Kellogg (1953).

amplitude of the pressure waves and the displacement waves, from a pulsating bubble, which he indicates as a convenient measure of the range of the usefulness of near-field effects, were calculated from the expression

$$n = \lambda/2$$

where n = the distance of the point of equal amplitude from the point of origin.[5] The values obtained are, of course, rather rough approximations, but are fully adequate for the present discussion. The data on the temperature range at which *Galeichthys* is sonic are original, having been established for a certain locality in connection with another project, only vaguely related to studies on schooling. Differences in the attenuation of the various wavelengths concerned are not significant within the spread of frequencies here discussed (Albers, 1960). At much higher frequencies, that is, within the k Hz. range, there is some differential absorption, but this is far removed from the sounds fish usually produce. It should be emphasized, however, that these calculations do not include the influence of the absolute energy of the original signal which, of course, can be of great importance.

Since the range of hearing in fishes has been calculated in general terms to run from about 100 to 3,000 Hz and the range important to the lateral-line organs from about 20 to 500 Hz (Harris, 1964), it follows that the statements made here all fall within the accepted range of fish auditory powers. Also, that when the producer is separated from the receiver, ". . . both near-field and far-field effects must be considered for the organs of hearing as well as the organs of the lateral line." At a frequency of 25 Hz, the wavelength is about 200 feet and at 1000 Hz it is about five feet.

From the preceding it should be possible to estimate at about what distance a fish would lose the directionality of, say, the percolator sound by knowing the frequencies and temperatures involved. Tavolga (1960) stated that there was a predominance of frequencies around 300 Hz in these sounds, and his sonogram indicated that they ranged to below 100 and above 800 Hz. If a fish loses its sense of directionality at about the distance calculated, then if a fish was receiving cues from a *Galeichthys* producing the "percolator" sound at a frequency of 300 Hz or higher, it would not be useful beyond something less than three feet. However, in the spectrum of this sound there are abundant frequencies of 200 and some of less than 100 Hz. Presumably these would be considerably more attenuated at their respective ranges which are about three and one-half and eight feet. At a frequency as low as 25 Hz the range reaches some 30 feet, and one may assume that there are some effective frequencies between these two extremes, at perhaps ten to 20 feet from the sound source. At this distance the ability to receive directional cues, especially at night, could be of great value, as will be developed, especially since there is some observed behavior of fishes that may be accounted for by a range similar to the one given above. In a personal communication, Dr. Tavolga indicated that he has also observed differences in the behavior of both "lost" schooling fishes and predators that could perhaps represent a passing out of or into the limits of the near-field.

Other influences

Other sensory modalities, such as olfaction or taste, would not seem to be importantly involved in the interactions of schooling fishes and their predators, if at all, or at least there is no clear evidence or theory which would indicate such involvement. Brock and Riffenburgh (1960) considered olfaction a possibility, writing, ". . . predators may attempt to remain with a school of prey even though satiated, and it is not unlikely that a large school of prey may leave an easily detectable trail of odor for a predator to follow," but present no data to support this opinion. Skinner, Mathews and Parkhurst (1962) concluded that the *Schreckstoff* effect served to warn other members of a school, because ". . . alarmed fish communicate fright by releasing a chemical substance into the water." This statement was questioned by Williams (1964) as follows, "Why then for communcating a message for which speed of reaction would be especially important, would fishes rely on the slow process of chemical diffusion?" With apparently a single exception, the *Schreckstoff* reaction is confined to the Cypriniformes, an almost entirely freshwater order. This group does exhibit some schooling, usually in a facultative form. Fishes of this group are not to be considered as obligate schoolers. Strangely, in this connection, Thines and Vandenbussche (1966) indicate that in *Rasbora* the alarm substance is more effective in the daytime, even in a dark room. Pfeiffer (1962) has reviewed the entire subject of the "fright reaction" and his analysis indicates it to be rather remote from the present problem.

Breaks in ontogeny, or more properly, points at which step functions occur, such as in the case of certain fishes, pelagic from hatching,

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[5] n is expressed in the same units used to measure wavelength.

when they reach a sufficiently advanced but still transparent post-larval stage, and encounter shallow water, will permanently change their attitudes, develop pigment and settle close to the bottom. These, at this time, usually break up their schools into single individuals or small parties, as the life history unfolds. This type of ontogenetic change seems to be present in a life history where one stage is required to vanish abruptly, so that the species concerned either becomes a permanent schooler or abandons the habit entirely.

THE STRUCTURE AND SIZE OF SCHOOLS

Brief reference has already been made to the range of visibility under water and the relation of the conspicuousness of fishes to its degree of transparency. Here a return is made to that subject and its more immediate implications. Because of the considerable mathematical difficulty of dealing with three-dimensional structures of complex outline, see Cullen, Shaw and Baldwin (1965), the case of a simple surface type school, which is often not more than one or two fish deep, will be discussed for illustrative purposes.

It is not merely accidental that most fusiform fishes, not in a school, usually face toward any disturbance less than one that instigates immediate flight. Aside from visual demands in an animal that cannot turn its head alone, there is an immediate reduction of conspicuousness, as the frontal view is much less conspicuous than the corresponding lateral aspect. Anyone who has operated under water is well aware of the phenomenon of having a fish effectively disappear before one's eyes merely because it had turned so as to point at the observer. Such turning to face a disturbance is much less likely in the case of a chunky fish such as an ostracid or diodontid in which such a maneuver would do little to alter its aspect. These, moreover, are distinctly non-schooling types.[6]

The shape of schools

Since circles and spheres enclose the maximum amount of area or volume respectively for a given perimeter or surface, it follows that these or other shapes have a distinct bearing on the conspicuousness of fish schools and aggregations. For these reasons it could be argued that the commonness of such approximations as are found in real schools is a result of selection. As has, however, been indicated in other connections, it happens that many non-living systems show the same kind of behavior which depends only on their innate cohesiveness. That is, a drop of suitable oil in water of the same specific gravity will be found to be spherical or a drop of mercury on a flat surface will be found to be a badly deformed sphere, flattened on one side and of other curvature on the top side. In other words, departures from the form showing minimum surface may be considered as a measure of some special influence. In this sense the spherical schools discussed by Breder (1959) and the flowing schools of Breder (1951) all could be following simple physical influences, with the first presenting the least conspicuous form possible and the second exposing a much greater area. The latter are usually seen in very shallow water, commonly shallow enough to eliminate the species' predators. Also with the bottom and water surface so close together only globular groups of small size could occur, as for instance the globular pods of *Plotosus* reported by Knipper (1953 and 1955) and observed and discussed by Clark, in a personal communication. However, large sheet-like schools can naturally "fit" most easily into such vertically limited environments. Where this dimension is greater, schools tend to deepen, culminating in approximate spheres of some bulk. Here also larger predators may swim and view such gatherings from greater distances, up to the point where visibility ceases and the schools have protection not so much based on their own geometry as on the peculiarities of underwater vision. Springer (1957) considered huge schools of small fishes, whose bulk at a little distance could resemble some single large creature, to have a discouraging influence on possible predators. This would represent a case where visibility instead of invisibility became of positive advantage to the schoolers.

The problem of enormous schools

Data on details relevant to the present studies are not yet available on the truly huge schools, often involving many thousands of fishes, as exemplified by the great assemblages which are frequently formed by *Clupea* and *Scomber*. Suggestive information, however, would seem to indicate that they are not as uniform in their size composition as smaller schools are usually seen to be. It is conceivable that such lack of uniformity may be based on the manner in which they develop. If so, it may be that they represent an agglomeration of all the smaller schools in a given area. If, say, several hundred schools, each normally uniform in size range within itself, merged with others acceptably similar, it could cause the assembled mass to show a larger variation, from place to place

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[6] All these comments are related to the less specifically expressed view of Allee *et al.* (1949) and Allee (1951) on the reduction of total area exposed by fishes in a school.

within the whole group. If the combined schools mixed sufficiently, large fish encountering much smaller ones, a disruptive influence could develop, or at least induce an internal realignment so that the large fish were somewhat restricted to one part of the group and the small to another part, with intermediate fishes bridging between them. Then more or less temporary gradients in respect to size, or other characteristics, could develop and stream about within the group, establishing a continual movement driven by the realignment activities of all individuals. This sort of continual adjustment, with respect to locomotor facility is actually to be seen, on a much smaller scale, in smaller schools, and Breder (1965) thought that it formed the basis of the continual small adjustments found in most ordinary schools. This could easily lead to a shearing action breaking up the different size-groups into smaller, but still large schools. Such effects may in fact be responsible for the eventual disintegration of gigantic schools.[7] Also, it has been shown by Hunter (1966) that angular divergencies between school members are greater between individuals of greater variation in size.

Milanovskii and Rekubratskii (1960) performed some experiments with *Phoxinus* that have an indirect bearing on the preceding comments and on the amalgamation and disruption of groups composed of merely facultative schoolers, as follows.

"We noted that under natural conditions, several schools of minnows which fed in the same place, and which appeared from the outside to be one unit, reacted differently to changes of the surrounding environment. In the beginning of our observations, a school of small minnows was feeding; then a school of larger minnows approached cautiously, followed by the school of largest minnows, even more cautious and rapid than the fish of the first two schools. All the fishes, small, medium and large, mingled together and had we not seen them approaching gradually we might have considered them to be a single school. However, after some time, the large minnows hid behind the nearest stone, which they found somewhat downstream. From their hiding place, they swam to the food, grabbed it, and swam back. Such a phenomenon of utmost cautiousness in the search for food we designated by the term "withdrawal." At the slightest movement of the observer, the large minnows swam away, while the small and medium-sized ones continued to feed undisturbed. When the experimenter stretched his hand over the feeding spot, the school of medium-sized minnows fled while the smallest remained, fleeing only after the hand was immersed in the water. Thus, fishes of three different schools reacted in different ways to changes in the environment, while fishes belonging to each of the three schools reacted as one whole. The natural movements of fishes, obtaining food, fleeing in the face of danger, etc., have definite signal values (of different orders of importance) for the remaining fishes of the school. Among these movements one can distinguish between searching movements, alimentary movements and movements of fear." Also they wrote, again of fishes in a stream, "The strongest biological signal is the natural movement of fear. If, being frightened by something, one or several fishes move aside, the whole school follows them. We tried to give the fishes food in such small quantities that only one or two fishes could obtain it. Once satiated, these specimens became more fearful and went to shelter; they were followed by all the other, still hungry, fishes."[8]

The bearing that the various preceding notes have on ideas concerning the survival value of schooling is, among others, as before intimated, that such massive groups may have a deterrent influence over approaching predators.[9] However, it is also reasonable that such an influence would wane in a short time, to be replaced by an opposite one based primarily on habituation of nearby predators to such tremendous schools. The slow drawing in of predators from perhaps a considerable distance would be expected to follow, because individuals of the prey species concentrated in one place in an enormous mass would proportionally restrict their numbers elsewhere. Thus, a situation of positive survival value could transform to a negative one, and possibly also could become a force for the disintegration of the huge group.[10]

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[7] The finding of Allee and Dickinson (1954) that when a *Mustelus* was as little as 6.7 per cent smaller than another, the lesser dogfish would avoid the greater. This does not imply aggression on the part of the large fishes. This kind of avoidance is basic to the matters discussed above.

[8] These observations are also related to those of Breder (1965) on the feeding of schools of very small *Mugil*. The avoidance reactions these workers described is, no doubt, caused at least partly by the general refusal of fishes of slightly different sizes to mix.

[9] Such a situation is probably related to or identical with the "confusion effects" of Allee *et al.* (1949) and Allee (1951). Also related to this is evidence that fishes eat more when in groups than when alone (Allee, 1938).

[10] According to the English translation of Nikolsky (1963), the Russian usage is to apply "shoal" to such large groups as those here under discussion and to limit "school" to groups so small that presumably all members could have visual or other contact with every other member. In English and American usage "shoal" has apparently always been used as a synonym of "school."

The maximum advantage, then, is enjoyed by relatively small groups; that is, with additions of a few fish to a small group, the conspicuousness of the assemblage increases at a much smaller rate than does the number of its members. This advantage is lost, however, when the number becomes so vast that the volume occupied by the group, although remaining proportional to the number of individuals, becomes a conspicuous mass in terms of absolute size.

These various factors are necessarily influential in limiting the sizes of fish schools. Field observation demonstrates that in a wide variety of species this vague but very real "limit" is not very large, at least under normal circumstances. Although Breder (1965) could find no theoretical upper limit to the size that a fish school might attain on a hydrodynamic basis, such limitation may well be rooted in the aspect here under consideration.

Williams suggests that the tendency for schools to increase in size without limit until ". . . the advantages of increased gregariousness would be balanced by some disadvantage, such as depletion of food in the center of a school." This is something that under ordinary conditions would call for an extremely large school because of the internal churning of schools, exposing first one and then another of its members to the periphery as well as the general conditions of having the school move about or holding a position in a flow of water through it.

MacFarland and Moss (1967) were able to measure dissolved oxygen within and outside of large schools of *Mugil cephalus* Linnaeus. They report that there was a reduction of the oxygen concentration within the schools. Also that there were areas of disruptive activity in the locations showing the lowest oxygen readings. These areas sometimes broke up into several smaller schools. They refer such intraschool activity to oxygen depletion, carbon dioxide increase and pH reduction. As they indicate, this could account, at least in part, for such behavior and may be a factor in limiting school size on a basis of respiratory need.

Here the problem of mill formation originally analyzed by Parr (1927) and extended by Breder (1965) is pertinent. Does mill formation actually have deleterious[11] effects on the fish in a school or is an occasional occurrence of it without significant effect on them, making an interest in mills merely a matter of the mechanics of its origin and eventual destruction? This will have to remain an unanswered question, as so far there appear to be no facts or ideas that could begin a structure of theory building.

THE RELATIVE SIZE OF PREY AND PREDATOR

The manner of feeding of predators on schools would seem to have a distinct bearing on the success of the school as a survival device. Commonly predator fishes may be seen to dash into a school and pick off an individual member and immediately retreat, usually swallowing the fish whole. The predator seldom takes more than one fish at a time, but returns again and again, apparently until satiated. Typical examples of this type of predator are *Caranx*, *Tylosurus* and *Sphyraena*. This type of feeding is probably the least disruptive and the most conservative of the predators' food supply.

Other manners of feeding on schools, as that shown by *Pomatomus*, is destructive of much more of the food supply than that described above. Commonly an individual *Pomatomus* or small group of them will race through a school of smaller fishes, snapping right and left while they go, leaving a trail of half-fish behind. Usually it is the anterior end that is left, and this probably means that less than half of each fish destroyed becomes food for the predator.[12] Similar modes of "wasteful" feeding on schooling fishes have been described by Rich (1947) for *Xiphias*, and Breder (1952) for *Pristis*. Wisner (1958), however, exonerates *Makaira* from such destructive activity, as flailing about with its elongated rostral process in a school of much smaller fishes.

In fishes the ratio of the size of prey to predator may vary widely, ranging from extreme cases where the predator may be more than 20 million times the weight of its normal prey's weight, as for instance *Manta* preying on near microscopic plankton.[13] From this extreme the ratio ranges to unity or even to cases in which the prey may be larger than the predator, as in *Histrio* and the extreme example of *Chiasmodon*. This range of differences in size has a bearing on the nature of the utility of schooling.

The phenomenon of herding, for instance,

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[11] These could be extrinsic, possibly leading to greater predation for instance, or intrinsic, holding the fish uselessly or dangerously in a place of poor feeding or other disadvantage.

[12] These mutilated fish-remains usually become food of other types of fishes or invertebrates which otherwise would be scavenging for other organic matter. Occasionally some of them survive but are no longer members of the schooling population. See Breder (1934) and Gunter and Ward (1961) for records of this sort.

[13] Based on a *Manta* of 3,000 lbs. compared to a plankter of 0.1 oz., which is probably much too heavy for the average plankton organism. The value given for the difference in size is certainly minimal, possibly even 3 to 5 times too small.

can only take place within certain relative size ranges between prey and predator, for if the two be of approximately the same size, the predator's approach becomes one of stalking, and if the prey is vastly smaller, as above noted for *Manta,* it becomes a matter of ranging about in search of streaks of plankton where neither stealth nor herding is involved.[14]

SCHOOLS, THEIR MODELS AND DISCUSSION

The only serious mathematical treatment of the possible protective value of schooling has been presented by Brock and Riffenburgh (1960). See also Brock (1962) for supplementary data. This was followed by a note from Olson (1964) who called attention to the work of Koopman (1956a and b and 1957). The latter, which is concerned with the development of "the theory of search" from the mathematical approach, discusses cases involving situations where both target and searcher are moving, as in naval battles. Olson recognized the identity of this with the situation of prey and predator, especially among oceanic fishes. The contributions of both Brock and Riffenburgh, and Koopman are given in convincing mathematical terms.

The usage of the word "school" by Brock and Riffenburgh and by Olson is different from the usage here employed, both in implication and in context. In their usage, a school of fish covers both schools and aggregations as here used, irrespective of the individual orientations or the distances between individuals, up to the limit of the range of visibility and without reference to the drives and circumstances that created the group.

As the equations of Brock and Riffenburgh do not take the orientation of individuals into account, they apply equally well to either polarized or non-polarized assemblages. One of the marked characteristics of schools, in the present sense, is that they consist of individuals spaced a "standard" distance apart. Thus equation (28) of Brock and Riffenburgh is applicable to schools only when c, the distance between individuals in the group, is very small, for if it becomes large, the polarization loosens and the group can no longer be recognized as a closely ordered array of fishes, all swimming side by side in a common direction. This distance, (axis to axis between adjacent fishes) is usually from one-half to three-quarters the length of the individuals (Breder, 1954, 1965).

The whole possible confusion is further complicated by the fact that Brock and Riffenburgh, although dealing with ". . . assumptions . . . and conclusions . . . not related to the observed behavior pattern of any particular species of fish . . . ," obviously are concerned primarily with scombriform fishes, a group with which the senior author of that paper has had wide experience. These fishes form excellent material for such studies, being one of the notable schooling groups. It so happens, however, that as many of these species age they tend to lose their strong propensity to school. Consequently, at least in the larger species such as *Thunnus,* the giant-sized individuals occur as solitary fishes or at least do not form the tightly organized schools of their youth. Large fishes in general tend less toward schooling than do small ones. This may be associated with the fact that the larger the fish, the less likely it is to fall prey to some predator of still larger size. Certainly if schooling serves a protective function, the above should naturally follow.

Lest any of the above comments be thought a criticism of a very thoughtful piece of work, this is to emphasize that these remarks are given here only as a warning to the reader to beware of possible misunderstanding because of differences in the usage of terms.

Koopman (1956a and b, 1957) divides his work into three parts, which he describes as follows. "I. The kinematic bases, involving the positions, geometrical configurations, and motions in the searchers and targets, with particular reference to the statistics of their contacts and the probabilities of their reaching various specified positions. II. The probabilistic behavior of the instrument (eye, radar, sonar, etc.) when making a given passage relative to the target. III. The over-all result—the probability of contact under general stated conditions, along with the possibility of optimizing the results by improving the methods of directing the search." Koopman considers much of his theory concerned with the probability of situation to be a special case of the theory of stocastic processes. Obviously much of this has direct bearing on predator and prey relationships, especially as displayed by open water fishes.

Both Brock and Riffenburgh, and Olson express regret for the small amount of field data available to compare with mathematical models. The former wrote, "The general lack of field data concerning the behavior pattern for a prey species and its predator renders either the confirmation or refutation of conclusions reached

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[14] See Bigelow and Schroeder (1948) for a discussion of herding in *Alopias* and Hiatt and Brock (1948) for a discussion of it in *Euthynnus.* More complex prey-predator relationships are described by Springer (1957) for *Rhincodon* and others, by Fink (1959) for Porpoises and *Sardinops* and by Bullis (1961) for *Carcharinus longimanus.*

in this paper by the elaboration of some scheme of predator strategy rather futile." The latter wrote, referring to the Koopman equations, "These are two basic equations, but to put reasonable numbers in them is another matter." For similar reasons, no attempt will be made here to apply any of these equations. Our intent is to bring together the mathematical and observational aspects of work on fish schools, to present some field observations hitherto unpublished, and to give some general considerations on the whole matter.

Although there is a large literature on prey and predator relationships, almost none of it is concerned with features that would seem to have bearing on the problems of fish schools. The work on bird flocks, such as those formed by starlings, indicates that these are evidently operating in a similar manner about as closely as could be expected, considering the large basic differences between birds and fishes, see for instance Horstmann (1950).

In discussing the possible evolutionary course of the schooling habit Williams wrote that ". . . the lack of any apparent functional organization is an eloquent argument for the conclusion that the properties of schools have not been established by natural selection on a basis of survival values." By "functional organization" Williams means any or all specializations such as "alarm notes," markings displayed in flight, *et cetera*. His detailed comments on the above are followed by, "Evidence for such mechanisms in fish schools would invalidate my position on their lack of functional organization." This extreme position is here considered, at least, premature, as there are a number of valid instances when just such mechanisms seem to be indicated. Considering the difficulties in obtaining adequate data and in interpreting their significance, the slow progress in this direction is not surprising. Relevant evidence suggestive of just such "functional organization" is to be found in practically all the current work on sound production among aggregating and schooling fishes, such as seen in Fish (1954), Kellogg (1953), Moulton (1956, 1958, and 1960), Tavolga (1958a, b, c and 1960), Marshall (1962), Stout (1963a and b), and Winn (1964). The consenus of these workers is in general that there are two primary functions provided by the sounds produced by fishes, evidently being either of sexual or social significance. The evidence that sound production is relevant to organization is indicated by various schooling fish that become sonic only at night, when the visual system is inoperable or only feebly so (Takarev, 1958; Shishkova, 1958; Moulton, 1960; and Marshall, 1962).

Bearing on the question of functional organization of fish schools are recent, more refined measurements of the spacing of individuals in a school that have shown that both extrinsic and intrinsic influences can vary these distances. John (1966), working on *Tilapia nilotica* (Linnaeus) and *Notemigonus crysoleucas* (Mitchill), for instance, showed that at very low light levels, below 10^{-3} f. c., schools tended to break up and that individuals served as, ". . . mutual distractions for one another and also as sources of fright." Previously, it had been thought that schools in little light broke up merely because of visual difficulties. This indicates that there is a positive repelling factor involved, that appears as light fades.

Hunter (1966), by means of computer techniques, showed that schools of *Trachurus symmetricus* (Ayres) deprived of food swam at greater distances from each other than did the same fishes after feeding. Although schools and aggregations appear to be leaderless, there are some special cases, such as a white *Carassius* being the focal point for aggregating by yellow companions (Breder, 1959).

There is no disagreement with the William's view of how schools may have arisen, namely ". . . that schooling could be expected to arise in any species subject to aggregation." In accordance with Williams' definition of schooling, this means, in effect, that fishes drawn to a given area by some non-social influence may then in some cases become social. He also wrote, ". . . that a school is not an adaptive mechanism itself, but rather an incidental consequence of adaptive individual behavior. The adaptation is the reaction of each individual to the school."

It seems most likely that schooling in fishes arose from a wide variety of causes, including some that are purely mechanical (Breder, 1965). Further speculations on this matter would seem hardly to be worthwhile, until some time when data and theory have reached a higher level of development.

Evidently the schooling habit becomes established because of purely mechanical or biological reasons, but it would certainly be expected that gene flow could re-enforce the habit, if it proved to be advantageous to the group.

Levins (1962, 1963, 1964) expresses the idea that the adaptive significance of gene flow is that it permits appropriate response to long-term general fluctuations of environment, while ". . . damping the responses to local ephemeral oscillations." This undoubtedly has bearing on the distribution of fish assemblages of all kinds. Levins indicates that migration tends to increase the above condition. It is noteworthy in this connection that obligate schooling forms generally have a large geographic range, produce large numbers of young and commonly show migratory movements. The population density is, of course, extremely high within the limits of the close confines their schools delimit. It is, however, extremely thin if their numbers are considered in reference to the huge areas the schools pass over, even more so if extensive migrations are involved. The fact of schooling precludes nest building or other protective reproductive modes that presumably permit the production of fewer young. The formation of great schools, and their subsequent dissolution, as discussed herein, may well exercise a regulatory role in the gene flow of the species involved.

All that precedes in this paper could be used to support the view that the functioning of prey-fish schools, as well as of unpolarized aggregations, represents just another method of attaining a manner of behavioral homeostasis. This implies that schooling is effective against excessive predation through a wide range of activities, but fails when various limits are exceeded. Backed up by adjustment of reproductive potential, all under the control of selective processes, including those of both predator and prey, as parts of a dynamic system, it is evidently sufficient to produce a situation of considerable stability in the observed populations. While these systems are probably not as closely controlled as, for instance, the hydra populations of Slobodkin (1964), it would be extremely difficult to attempt such analysis and experimental procedures on schooling fishes as he gives his material. Nevertheless, it would seem that the basic activity is similar. This view accepts schooling as a biologically useful activity seen against the appropriate ecological background.

SUMMARY

1. The range of sight, limited as it is by transparency of the water and the amount of light present, governs the effectiveness of schooling as a form of predation control, which varies widely with environmental features.

2. The geometry of the school shape and its motion affects the conspicuousness of schools where water transparency permits good visibility.

3. In situations where visibility is not a limiting factor, the system presents the degenerate limit where schooling fails to protect effectively.

4. The general quietness of fish schools, except under special conditions where some sound may be inevitable or others in which it may be desirable, suggests that there may have been suppression of sound in schooling fishes, probably by way of selection.

5. The physical form and attitudes of the constituent fishes bear on the effectiveness of schools as a protective device, as do the shape and motion of them, schooling being associated chiefly with streamlined fishes, less often with chunky or odd-shaped fishes.

6. Sufficiently large schools may act as a repellent to predators because of their size and shape.

7. School size is related to the availability of fishes of sufficient similarity of size to compose a coherent group, as well as the mechanics of flow within the group, and to this extent becomes amenable to treatment by hydrodynamic means.

8. The size of the predators relative to thc size of the prey leads to "stalking" if the sizes are about equal and to planktonic sifting if the prey is extremely small compared with the predator.

9. The whole matter of schooling and aggregating is looked upon as a mechanism of behavioral homeostasis and as such is subject to the influences of selective processes.

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